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Chemical Regulation of Growth, Yield, and Digestibility of Alfalfa and Smooth Bromegrass

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Abstract. In addition to enabling manipulation of plant growth and development, growth regulators have potential for increasing forage digestibility. This study focuses on the use of gibberellic acid (GA3), α-naphthalene acetic acid (NAA), 6-benzylaminopurine (BA), *o*-benzylhydroxylamine (OBHA), and monocetyl phosphate (C16P) to alter growth, dry weight (DW) yield, and in vitro digestible dry matter (IVDDM) of forage grasses and legumes grown in a greenhouse. Screening experiments revealed that GA3, NAA, and OBHA at rates of 1.6, 160, and 0.51 g a.i. ha^{-1}, respectively, were more effective in altering regrowth of potted alfalfa (*Medicago sativa* L.) and orchardgrass (*Dactylis glomerata* L.) compared with other treatments. Subsequent experiments with increasing dosages of GA3, NAA, and OBHA on alfalfa and smooth bromegrass (*Bromus inermis* Leyss.) confirmed that these regulators can be used to manipulate forage growth. Increasing concentrations of GA3 increased growth and DW yield but decreased IVDDM, whereas high concentrations of NAA decreased growth and DW yield but increased IVDDM. OBHA treatments resulted in little or negative change in IVDDM. Results generally showed that plant growth regulators can be used to manipulate forage growth, but that there is a trade-off between herbage yield and digestibility of forage tissues.

Chemical regulation has the potential to increase yield and improve digestibility of plants. Digestibility, which is greatly affected by cell wall and cell-wall component concentrations (Van Soest and Robertson 1980, Waldo 1985), is a fairly new target in growth-regulator research. Recent research has revealed that growth regulation can improve digestibility of grasses (Fales et al. 1990, Glenn et al. 1980, McGrath 1986, Roberts and Moore 1990, Sheaffer and Marten 1986) and manipulate the quality and yield of grass–legume mixtures (Fales and Hoover 1990, Fales et al. 1990). Lignin, which inhibits forage digestibility (Buxton and Russell 1988, Harkin 1973, Jung and Deetz 1993), shows natural variation (Grand et al. 1982) and has been successfully decreased by selective breeding (Buxton and Casler 1993). These types of experiments have provided an incentive for studies on the inhibition of lignification through application of plant growth regulators (Buck et al. 1989). Molecular structure and component integration of plant cell walls have been addressed (Bidlack et al. 1992, Chesson 1993, Jung and Deetz 1993) and growth-regulator research is one method to help understand these concepts and their applications to forage digestibility. Investigations thus far have generally shown that the quality of grasses and grass–legume mixtures can be improved, but only at the risk of lowering yield. Further investigations are needed to evaluate the action of commercial growth regulators on legumes and grasses, and to study the effects of natural plant hormones on pure grass and legume yield and quality.

Three plant growth regulators and two experimental chemicals were used to study fundamental growth responses in forages and to determine whether or not forage quality can be manipulated without sacrificing yield. The plant growth regulators used were gibberellic acid (GA3), which stimulates internode elongation and has been used to increase shoot length in corn (*Zea mays* L.; Rood et al. 1990) and increase yield of bermudagrass [*Cynodon dactylon* (L.) Pers.; Karnok and Beard

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1983] and rice (*Oryza sativa* L.; Revilla et al. 1988); α-naphthalene acetic acid (NAA), an auxin that causes cell elongation and has been used to increase yield in corn, spring wheat (*Triticum aestivum* L.), sugar beet (*Beta vulgaris* L.), and radish (*Raphanus sativus* L.; Wort and Patel 1970), as well as to inhibit growth at high concentrations (Gardner et al. 1985); and 6-benzylaminopurine (BA), a cytokinin that causes cell division and has been used to regulate fruit set in wheat (Dybing and Lay 1981) and soybean [*Glycine max* (L.) Merr.; Crosby et al. 1981]. Experimental chemicals were *o*-benzylhydroxylamine (OBHA), a lignin inhibitor (Hoagland 1985), and monocetyl phosphate (C16P), which has been shown to stimulate growth in wheat seedlings (Bidlack and Ohlrogge 1988).

Screening of these five plant growth regulators preceded dosage studies with the three most effective growth regulators. The first objective, pursued in the screening experiment, was to identify chemicals that have the greatest effect on forage growth, yield, and digestibility. Subsequent experiments addressed the second objective, which was to determine whether or not selected growth regulators, and concentrations thereof, can significantly affect growth, yield, and digestibility of alfalfa and smooth bromegrass. The third objective was to evaluate correlations between growth and digestibility of forage herbage, as affected by growth regulator treatments.

Materials and Methods

General Growing Conditions and Chemical Applications

Plants were established and maintained at the Iowa State University Agronomy Greenhouse (Ames) in 25-cm-diameter pots with a capacity of 3.8 L. Each pot was maintained to represent regrowth from either 3 legume plants or 10–15 grass plants, arranged as a sward of forage at the time of chemical application and harvest. Pots were watered as needed and fertilized once a week with Hoagland solution. Each pot contained a 1:2:2:4 mixture (by volume) of sand, Webster silty clay loam (fine-loamy, mixed, mesic Typic Haplaquolls) soil, peat, and perlite. One pot represented an experimental unit in both experiments. In the screening experiment, four replicates contained two species and six treatments for a total of 48 pots. The four replicates in the dosage experiment contained two species, three treatments, and five dosages of the treatments for a total of 120 pots. Greenhouse temperatures during all experiments ranged from 20 to 37°C, and high-pressure sodium lamps supplemented sunlight to provide a 14-h day/10-h night regime.

Chemicals were obtained from Sigma Chemical Company[1] unless specified otherwise. All growth regulator applications were formulated by mixing or suspending the appropriate amount of chemical in 1.0 L of 1.0 mM NaOH with 5.0 mL of Tween 80 surfactant. Entire plants from each pot were sprayed with 20.0 mL of these formulations with a hand-held sprayer. Control plants were sprayed with the same formulations minus growth regulator. Plants in all experiments were sprayed at 2 and 4 weeks of regrowth.

Screening Experiment

Arrow alfalfa (*Medicago sativa* L.) and Napier orchardgrass (*Dactylis glomerata* L.) were established in the fall and cut twice before regrowth was used for chemical treatment. Concentrations of GA3, BA, OBHA, and C16P were chosen to stimulate growth, whereas a concentration of NAA was chosen to retard growth. Plant growth regulators and their applied rates were as follows: GA3, 1.6 g a.i. ha^{-1}; NAA, 160 g a.i. ha^{-1}; BA, 16.0 g a.i. ha^{-1}; OBHA, 0.51 g a.i. ha^{-1}; and C16P, 20.5 g a.i. ha^{-1}. The C16P was synthesized from cetyl alcohol according to Bidlack and Ohlrogge (1988). Plant material from all pots was harvested by cutting at 3 cm above the potting mix after 6 weeks of regrowth in the spring. Regrowth was measured by determining height and dry weight (DW) of both species, as well as alfalfa stem in vitro digestible dry matter (IVDDM) and orchardgrass total plant IVDDM.

Response to Dosage Experiment

Arrow alfalfa and Barton smooth bromegrass (*Bromus inermis* Leyss.) were established in the fall and cut twice before regrowth was used for chemical treatment. The three most effective growth regulators and their applied rates were as follows (control plants were also included as described above): GA3, 1.6, 3.2, 6.4, and 12.8 g a.i. ha^{-1}; NAA, 160, 320, 640, and 1280 g a.i. ha^{-1}; and OBHA, 0.51, 1.02, 2.05, and 4.10 g a.i. ha^{-1}. Plant material from all pots was harvested by cutting at 3 cm above the potting mix after 8 weeks of regrowth in the summer. Measurements made for both species included height, stem DW, leaf DW, total DW, leaf/stem ratio, stem IVDDM, leaf IVDDM, and total plant IVDDM.

Subsampling and Digestibility Analyses

Subsamples for the response-to-dosage experiment were obtained by dividing each pot into equal halves and harvesting one-half to represent total plant material and the other half for leaf and stem plant material. Each pot thus provided total, leaf, and stem subsamples that were dried, weighed, and analyzed for IVDDM. Once all data were collected, yield values from all subsamples were combined for statistical analyses on a per pot or DW basis.

Extent of IVDDM, as an indication of digestibility, was determined by the direct acidification method described by Marten and Barnes (1980). Rumen fluid was collected from a fistulated

[1] Mention of a specific trade name or vendor does not imply endorsement or criticism of similar products not mentioned.

Table 1. Mean values from four replications of greenhouse-grown forages treated with growth regulators after 2 and 4 weeks of regrowth and harvested at 6 weeks of regrowth.

	Alfalfa							Orchardgrass						
Measurement[b]	CTL[a]	GA3	NAA	BA	OBHA	C16P	LSD[c] (0.05)	CTL	GA3	NAA	BA	OBHA	C16P	LSD (0.05)
Height (cm)	82.3	95.5	58.6	82.8	83.1	87.8	10.6	47.7	51.9	45.1	45.3	51.1	51.1	4.7
Total DW (g)	34.6	36.9	26.4	33.7	35.2	33.8	2.6	21.3	21.7	20.6	21.3	22.1	21.3	2.0
Stem IVDDM ($g\ kg^{-1}$ DW)	600	592	564	583	589	576	29	—	—	—	—	—	—	—
Total IVDDM ($g\ kg^{-1}$ DW)	—	—	—	—	—	—	—	639	648	643	638	636	640	21

[a] CTL, control; GA3, gibberellic acid; NAA, α-naphthalene acetic acid; BA, 6-benzylaminopurine; OBHA, *o*-benzylhydroxylamine; C16P, monocetyl phosphate.
[b] DW, dry weight; IVDDM, in vitro digestible dry matter.
[c] Least significant differences (LSD) are calculated from standard error of the mean.

Table 2. Mean values from four replications of greenhouse-grown alfalfa treated with different rates of growth regulators after 2 and 4 weeks of regrowth.[a]

		GA3 ($g\ a.i.\ ha^{-1}$)				OBHA ($g\ a.i.\ ha^{-1}$)				
Measurement	Control	1.6	3.2	6.4	12.8	0.51	1.02	2.05	4.10	LSD (0.05)[b]
Height (cm)	117	122	128	127	133	127	118	128	126	16
Stem DW (g)	69	76	75	68	85	71	66	74	73	12
Leaf DW (g)	19	17	14	13	18	12	14	14	16	4
Total DW (g)	88	94	89	81	102	83	81	88	89	14
Leaf/stem ratio	0.21	0.18	0.15	0.15	0.17	0.15	0.18	0.16	0.18	0.04
Stem IVDDM ($g\ kg^{-1}$ DW)	540	560	540	530	540	520	540	540	520	33
Leaf IVDDM ($g\ kg^{-1}$ DW)	710	690	710	710	670	720	730	720	710	34
Total IVDDM ($g\ kg^{-1}$ DW)	600	600	590	600	600	610	610	560	560	39

[a] Abbreviations as in Table 1.
[b] Values are shown for foliage harvested at 8 weeks of regrowth and least significant differences (LSD) are calculated from standard error of the mean.

steer that was fed a diet of alfalfa–orchardgrass hay. Duplicate samples, from each experimental unit, were hydrated in buffer for at least 1 h before inoculation. Calculation of IVDDM was based on extent of digestion after total fermentation of the sample with rumen fluid for 48 h, followed by acid pepsin for 24 h.

Statistical Analyses and Graphical Representations

Analysis of variance (ANOVA) was performed separately for each species in both experiments. In the screening experiment, a randomized complete-block design was implemented for alfalfa and orchardgrass with treatment tested against residual error. In the dosage experiment, a randomized complete-block design was implemented for alfalfa and smooth bromegrass with the treatment × concentration interaction tested against residual error. Mean values and pooled standard error of the mean, used to calculate least significant differences (LSD), were generated by SAS PROC GLM (SAS Institute 1985). Differences were evaluated at the 0.05 and 0.01 levels of probability. Mean values within treatments (averaged over replicates) of the dosage experiment were used to show growth and digestibility in response to growth regulator concentration. Third-order regression liens, for growth regulator responses, were drawn by the computer program, SigmaPlot™. Mean values of pooled data from the dosage experiment were used to determine correlations between digestibility and forage growth. Correlation values, and their significance at the 0.01 level of probability, were determined by SAS PROC CORR (SAS Institute 1985).

Results and Discussion

Screening Experiment

Significant variation was detected in height, total DW, and digestibility of alfalfa, and in height of orchardgrass, as affected by growth regulator applications (Table 1). Compared with the control (CTL), GA3 increased plant height of alfalfa, but not of orchardgrass, and failed to modify DW or digestibility of either species. The NAA decreased height and DW of alfalfa and IVDDM of alfalfa stems. The OBHA, BA, and C16P failed to modify plant growth and digestibility, however; larger means for height and DW were obtained from

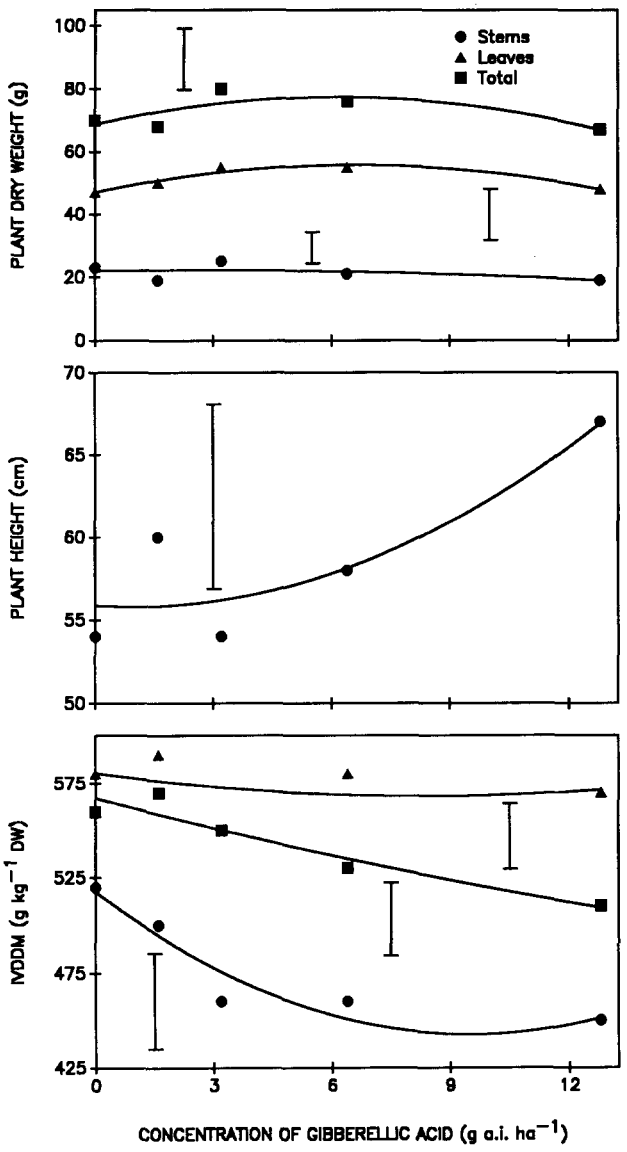

Fig. 1. Plant dry weight (DW), plant height, and in vitro digestible dry matter (IVDDM) of greenhouse-grown smooth bromegrass, treated with different dosages of gibberellic acid at 2 and 4 weeks of regrowth, and harvested at 8 weeks of regrowth. Each point represents the mean of four replications, and least significant differences at the 0.05 level of probability are shown.

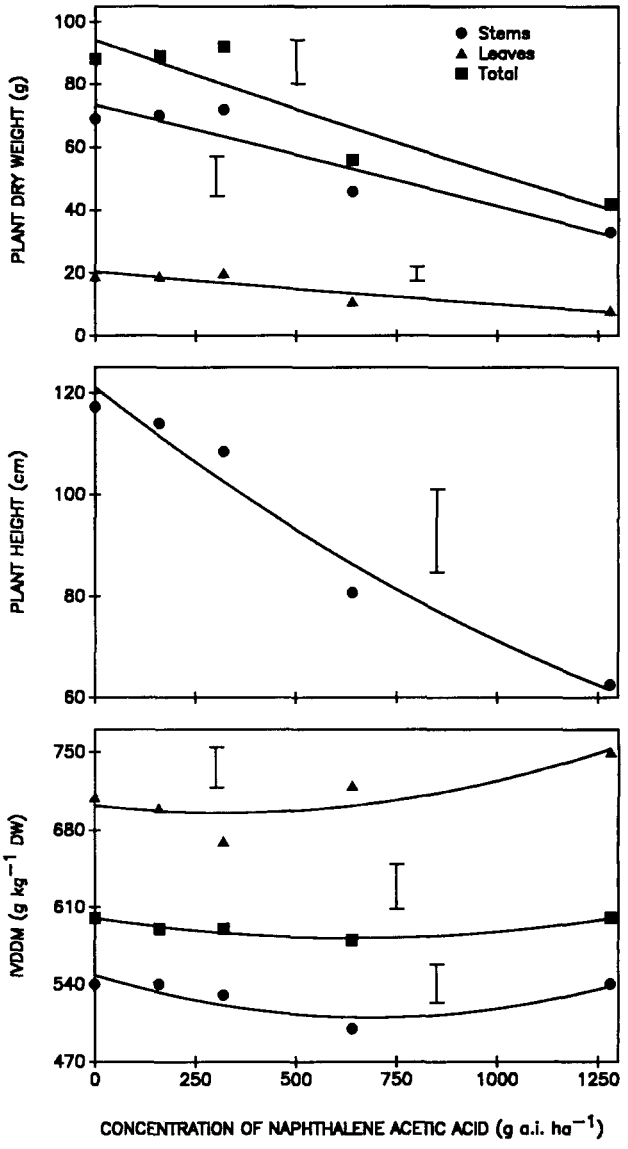

Fig. 2. Plant dry weight (DW), plant height, and in vitro digestible dry matter (IVDDM) of greenhouse-grown alfalfa, treated with different dosages of naphthalene acetic acid at 2 and 4 weeks of regrowth, and harvested at 8 weeks of regrowth. Each point represents the mean of four replications, and least significant differences at the 0.05 level of probability are shown.

OBHA compared with those from the control. Of the five growth regulators tested, only GA3, NAA, and OBHA were selected for use in the dosage experiment.

Because these screening studies revealed significant growth regulator responses from alfalfa and weak responses from orchardgrass, we decided to continue using alfalfa as the representative forage legume, but to replace orchardgrass with a grass that demonstrates stem-elongation growth habit. Orchardgrass may not have demonstrated dramatic growth regulator responses because this species was not vernalized, resulting in nonelongated vegetative stems. Smooth bromegrass, which does not require vernalization for initiation of reproductive tillers, replaced orchardgrass in subsequent experiments. Use of alfalfa and smooth bromegrass enabled our study of stem and leaf components. Responses of these species to growth regulators were studied separately because it has been shown that their rates of DW and cell-wall deposition are different (Bidlack and Buxton 1992).

Table 3. Mean values from four replications of greenhouse-grown smooth bromegrass treated with different rates of growth regulators after 2 and 4 weeks of regrowth.[a]

Measurement	Control	NAA (g a.i. ha^{-1})				OBHA (g a.i. ha^{-1})				LSD (0.05)[b]
		160	320	640	1280	0.51	1.02	2.05	4.10	
Height (cm)	54	48	52	53	58	50	49	53	54	11
Stem DW (g)	23	30	19	17	19	33	24	20	25	9
Leaf DW (g)	47	49	48	44	49	49	59	54	58	16
Total DW (g)	70	79	67	61	68	81	82	74	82	19
Leaf/stem ratio	3.1	2.9	3.5	3.5	3.6	2.3	3.6	3.8	3.4	1.0
Stem IVDDM (g kg^{-1} DW)	520	500	520	530	490	510	520	530	520	50
Leaf IVDDM (g kg^{-1} DW)	580	570	570	580	570	580	610	600	590	34
Total IVDDM (g kg^{-1} DW)	560	560	540	560	520	560	570	570	570	37

[a] Abbreviations as in Table 1.

[b] Values are shown for foliage harvested at 8 weeks of regrowth and least significant differences (LSD) are calculated from standard error of the mean.

Response to Dosage Experiment

Significant differences in growth (height, DW, leaf/stem ratio) and digestibility were detected as a function of growth regulator dosage for most treatments of alfalfa (Table 2 and Fig. 2) and some treatments of smooth bromegrass (Table 3 and Fig. 1). Except for OBHA treatment of smooth bromegrass, differences in growth were accompanied by differences in IVDDM within treatments of each species. These results imply a cause–effect relationship between growth and digestibility of forage as affected by growth regulator treatments.

The highest concentration of GA3 significantly increased height, increased stem and total DW, and decreased the leaf/stem ratio of alfalfa (Table 2). Increased total DW of alfalfa followed increased stem DW as a result of increasing GA3 dosage. Whereas increased stem DW and decreased leaf/stem ratio in legumes may correspond to lower IVDDM (Buxton et al. 1985), data in Table 2 indicate that GA3-induced morphological changes in alfalfa did not significantly alter stem or total IVDDM. However, GA3 did decrease leaf IVDDM. In smooth bromegrass, GA3 treatments increased height and decreased stem and total digestibility (Fig. 1). Increasing plant height in smooth bromegrass sharply contrasted with decreasing digestibility. Whether or not this decreased digestibility is completely attributable to increased stem mass, reorganization of stem cell-wall carbohydrates after GA3-induced loosening (Revilla et al. 1988), or combinations thereof, is not known. It is likely that GA3 stimulated growth and conversion of soluble carbohydrates to structural carbohydrates, thereby limiting digestibility.

High concentrations of NAA significantly decreased height and DW of all components and increased leaf IVDDM in alfalfa (Fig. 2). Negative effects of NAA on forage growth probably resulted from high applications of auxin beyond optimal rates for growth stimulation (Gardner et al. 1985). Decreasing yield paralleled decreasing plant height of alfalfa and contrasted with increasing leaf IVDDM (Fig. 2). High NAA applications may have slowed growth, caused more carbohydrate to remain in the soluble form, and thus increased digestibility. The NAA did not cause any significant changes in growth, yield, or digestibility of smooth bromegrass (Table 3). These results indicate that NAA produces an inverse relationship between growth and digestibility in alfalfa, and has essentially no effect on smooth bromegrass at the rates applied.

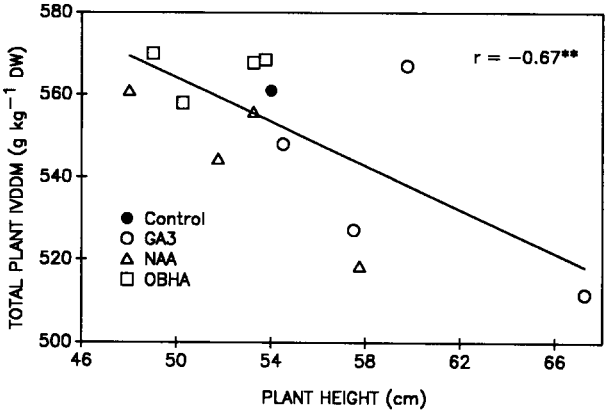

Fig. 3. Correlation between total plant in vitro digestible dry matter (IVDDM) and plant height of greenhouse-grown smooth bromegrass, treated with different dosages of gibberellic acid (GA3), naphthalene acetic acid (NAA), and *o*-benzylhydroxylamine (OBHA) at 2 and 4 weeks of regrowth, and harvested at 8 weeks of regrowth. Each point represents the mean of four replications. **Significant at the 0.01 level of probability.

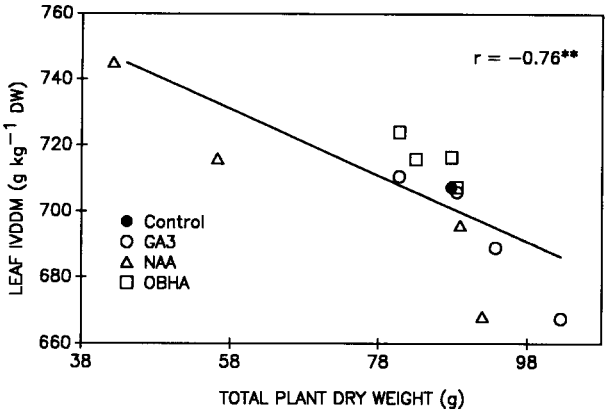

Fig. 4. Correlation between leaf in vitro digestible dry matter (IVDDM) and total plant dry weight of greenhouse-grown alfalfa, treated with different dosages of gibberellic acid (GA3), naphthalene acetic acid (NAA), and *o*-benzylhydroxylamine (OBHA) at 2 and 4 weeks of regrowth, and harvested at 8 weeks of regrowth. Each point represents the mean of four replications. **Significant at the 0.01 level of probability.

Compared with the control, OBHA did not stimulate growth of alfalfa, and, at a rate of 0.51 g a.i. ha^{-1}, decreased leaf DW and the leaf/stem ratio (Table 2). However, application of 0.51 g a.i. ha^{-1} OBHA to plants increased stem DW in smooth bromegrass compared with control plants (Table 3). Marginal changes in alfalfa and smooth bromegrass growth, as a result of OBHA application, did not improve the total digestibility of either species. As a general phenylpropanoid inhibitor, OBHA may have inhibited pathways not committed to lignin, such as anthocyanin and flavonoid metabolism (Hoagland, 1985), which may not directly affect digestibility. Application of the highest rate of OBHA decreased the total digestibility of alfalfa. Variation in components not measured probably led to the decrease in total IVDDM of alfalfa.

All concentrations of growth regulator treatments were combined to reveal a significant negative correlation between smooth bromegrass total IVDDM and plant height (Fig. 3). These results imply that taller smooth bromegrass plants exhibit less total forage digestibility. Data were also combined to reveal a significant negative correlation between alfalfa leaf IVDDM and total plant DW (Fig. 4). Negative correlations between DW yield and IVDDM have also been shown in cool-season grasses as a result of imazethapyr applications (Fales et al. 1990). Altogether, these results confirm a cause–effect relationship between plant morphology and digestibility. Taller and higher-yielding plants demonstrated lower digestibility.

Conclusions

Forage growth, yield, and digestibility can be manipulated by application of plant growth regulators. There was a trade-off between yield and quality when using the chemicals and concentrations used in this study. Increasing concentrations of GA3 increased growth and yield but decreased digestibility, whereas high concentrations of NAA decreased growth and yield but increased digestibility. OBHA treatments resulted in little or negative change in digestibility. More information is needed to explain the effects of these growth regulators on plant cell walls.

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